

Spectral properties of excitable systems subject to colored noise

Jannis Schuecker,¹ Markus Diesmann,^{1,2} and Moritz Helias¹

¹*Institute of Neuroscience and Medicine (INM-6) and Institute for Advanced Simulation (IAS-6), Jülich Research Centre and JARA, Jülich, Germany*

²*Medical Faculty, RWTH Aachen University, Germany*

(Dated: February 18, 2015)

Many phenomena in nature are described by excitable systems driven by colored noise. For systems with noise fast compared to their intrinsic time scale, we here present a general method of reduction to a lower dimensional effective system, capturing the details of the noise by dynamic boundary conditions. We apply the formalism to the leaky integrate-and-fire neuron model, revealing an analytical expression for the transfer function valid up to moderate frequencies. This enables the characterization of the response properties of such excitable units and the assessment of the stability of networks thereof.

PACS numbers: 05.40.-a, 05.10.Gg, 87.19.l

In his pioneering work Kramers [1] investigated chemical reaction rates by considering the noise-activated escape from a metastable state as a problem of Brownian motion over a barrier. As in the original work, subsequent studies (see references in [2]) assume the noise statistics to have a white spectrum. This idealization simplifies the analytical treatment and is the limit of non-white processes for vanishing correlation time [3]. White noise cannot exist in real systems, which is obvious considering, for example, the voltage fluctuations generated by thermal agitation in a resistor [4, 5]: if fluctuations had a flat spectrum, power dissipation would be infinite. In a non-equilibrium setting white noise can be replaced by external driving fluctuations characterized by a single time constant, representing a more realistic colored-noise model. This comes along with considerable difficulties, since it adds a dimension to the governing Fokker-Planck equation (FPE). The effect of colored noise is relevant in fluctuation-induced transitions observed in dye lasers, chemical reactions, turbulent transition and optical systems (see [6, 7] and references therein for applications). These transition phenomena have been studied in abstract terms as the mean first passage time (MFPT) of a particle in the Landau potential [8–13]. The effect of colored noise on the escape from a potential well is also relevant in modeling biological membranes: the leaky integrate-and-fire (LIF) neuron model with exponential synaptic currents can equivalently be described as a one-dimensional system driven by colored noise. Based on the work of Doering et al. [13] and Kłosek and Hagan [14], Brunel et al. [15, 16] calculated the high-frequency limit of its transfer function. Here we complement these works by a perturbation expansion in the flux operator appearing in the FPE itself. This approach leads to a general method to reduce a first order differential equation driven by additive fast colored noise to an effective one-dimensional system, revealing spectral properties of the system valid up to moderate frequencies. The effective formulation implicitly contains the match-

ing between outer and boundary layer solutions as well as the half-range expansion required to obtain the latter: colored-noise approximations for stationary but more importantly also for dynamic quantities are directly obtained by shifting the location of the boundary conditions in the white-noise solutions.

Consider a pair of coupled stochastic differential equations (SDE) with a slow component y with time scale τ , driven by a fast Ornstein-Uhlenbeck process z with time scale τ_s . In dimensionless time $s = t/\tau$ and with $k = \sqrt{\tau_s/\tau}$ relating the two time constants we have

$$\frac{dy}{ds} = f(y, s) + \frac{z}{k} \quad k \frac{dz}{ds} = -\frac{z}{k} + \xi, \quad (1)$$

with a unit variance white noise $\langle \xi(s+u) \xi(s) \rangle = \delta(u)$. We are interested in the case $\tau_s \ll \tau$. To formally derive an effective diffusion equation for y and to obtain a formulation in which we can include absorbing boundaries, we consider the FPE [17] corresponding to (1)

$$k^2 \partial_s P = \partial_z \left(\frac{1}{2} \partial_z + z \right) P - k^2 \partial_y S_y P, \quad (2)$$

where $P(y, z, s)$ denotes the probability density and we introduce the probability flux operator in y -direction as $S_y = f(y, s) + z/k$. Factoring-off the stationary solution of the fast part of the Fokker-Planck operator, $P = Q \frac{e^{-z^2}}{\sqrt{\pi}}$, we observe the change of the differential operator $\partial_z \left(\frac{1}{2} \partial_z + z \right) \rightarrow L \equiv \left(\frac{1}{2} \partial_z - z \right) \partial_z$, which transforms (2) to

$$k^2 \partial_s Q = LQ - kz \partial_y Q - k^2 \partial_y f(y, s) Q \quad (3)$$

and we refer to Q as the outer solution, since initially we do not consider boundary conditions. The strategy is as follows: we show that the terms of first and second order in the small parameter k of the perturbation ansatz $Q = \sum_{n=0}^2 k^n Q^{(n)} + O(k^3)$ cause an effective flux acting on

the z -marginalized solution $\tilde{P}(y, s) = \int dz \frac{e^{-z^2}}{\sqrt{\pi}} Q(y, z, s)$ that can be expressed as a one-dimensional FPE correct up to linear order in k . To this end we need to know the first order correction to the marginalized probability flux $\nu_y(y, s) \equiv \int dz \frac{e^{-z^2}}{\sqrt{\pi}} S_y Q(y, z, s) = \sum_{n=0}^1 k^n \nu_y^{(n)}(y, s) + O(k^2)$. Inserting the perturbation ansatz into (3) we have $LQ^{(0)} = 0$ and obtain for the first and second orders

$$\begin{aligned} LQ^{(1)} &= z\partial_y Q^{(0)} \\ LQ^{(2)} &= \partial_s Q^{(0)} + z\partial_y Q^{(1)} + \partial_y f(y, s) Q^{(0)}. \end{aligned} \quad (4)$$

With $Lz = -z$ the general solution for the first order

$$Q^{(1)}(y, z, s) = Q_0^{(1)}(y, s) - z\partial_y Q^{(0)}(y, s) \quad (5)$$

leaves the freedom to choose a homogeneous (z -independent) solution $Q_0^{(1)}(y, s)$ of L . Collecting all terms which contribute to ν_y in orders k^2 and higher in ι , the only relevant part of the second order solution is $-z\partial_y Q_0^{(1)}(y, s)$, which leaves us with

$$\begin{aligned} Q(y, z, s) &= Q^{(0)}(y, s) + kQ_0^{(1)}(y, s) \\ &\quad - kz\partial_y Q^{(0)}(y, s) - k^2 z\partial_y Q_0^{(1)}(y, s) + \iota, \end{aligned} \quad (6)$$

from which we obtain the marginalized flux

$$\nu_y(y, s) = \left(f(y, s) - \frac{1}{2}\partial_y \right) \tilde{P}(y, s) + O(k^2). \quad (7)$$

We observe that $f(y, s) - \frac{1}{2}\partial_y$ is the flux operator of a one-dimensional system driven by unit variance white noise and $\tilde{P}(y, s) \equiv Q^{(0)}(y, s) + kQ_0^{(1)}(y, s)$ is the marginalization of (6) over z . Note that in (6) the higher order terms in k appear due to the operator $kz\partial_y$ in (3) that couples the z and y coordinate. Eq. (7) shows that these terms cause an effective flux that only depends on the z -marginalized solution $\tilde{P}(y, s)$. This allows us to obtain the time evolution by applying the continuity equation to the effective flux (7) yielding the effective FPE

$$\partial_s \tilde{P} = -\partial_y \nu_y(y, s) = \partial_y \left(-f(y, s) + \frac{1}{2}\partial_y \right) \tilde{P}. \quad (8)$$

Effective FPEs, to first order identical to (8), but also including higher order terms, have been derived earlier [8–12]. These approaches have been criticized for applying white-noise boundary conditions to the effective system [14]. Further discussion evolved since an absorbing boundary either amounts to reaching a separatrix in the two dimensional domain [18] or to one component crossing a constant threshold value [19], depending on the physics of the system. Doering et al. [13] and Kłosek and Hagan [14] treated the latter by singular perturbation methods and boundary layer theory, showing that the $O(k)$ correction to the static MFPT stems from colored-noise boundary conditions for the marginalized density

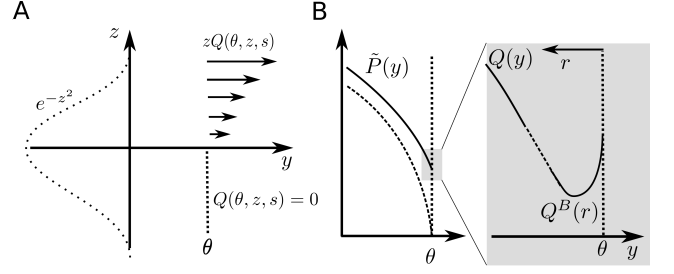


Figure 1. Boundary conditions. A: Flux and boundary condition in the two-dimensional colored-noise system. On the negative half plane $z < 0$ the density must vanish at threshold θ . B: Density of the white-noise system (dashed) vanishes at threshold. The density of the effective system has a finite value at threshold which is determined by the matching between the outer solution Q and the boundary layer solution Q^B (right).

of the effective system. Extending this approach to the transient case requires a time-dependent boundary condition for \tilde{P} or, equivalently, for $Q_0^{(1)}$, because we assume the one-dimensional problem to be exactly solvable and hence the boundary value of $Q^{(0)}$ to be known. Without loss of generality, we assume an absorbing boundary at the right end $y = \theta$ of the domain. The flux vanishes at this threshold for all points with negative velocity in y given by $f(\theta, s) + \frac{z}{k} < 0$. A change of coordinates $z + kf(\theta, s) \rightarrow z$ simplifies the condition to $\frac{z}{k} Q(\theta, z, s) = 0$ for $z < 0$. The flux and this half range boundary condition are shown in Figure 1A. The resulting boundary layer at θ requires the transformation of the FPE (3) to the shifted and scaled coordinate $r = \frac{y-\theta}{k}$

$$\begin{aligned} k^2 \partial_s Q^B &= LQ^B - z\partial_r Q^B \\ &\quad + G(\theta, r, s, z) k Q^B + O(k^3), \end{aligned} \quad (9)$$

with $Q^B(r, z, s) \equiv Q(y(r), z, s)$ and the operator $G(\theta, r, s, z) = f(\theta, s)(2z - \partial_z) - \partial_r(f(kr + \theta, s) - f(\theta, s))$. The boundary condition then takes the form $Q^B(0, z, s) = 0 \quad \forall z < 0$. With the perturbation ansatz $Q^B = \sum_{n=0}^1 k^n Q^{B(n)} + O(k^2)$ we obtain

$$\begin{aligned} LQ^{B(0)} - z\partial_r Q^{B(0)} &= 0 \\ LQ^{B(1)} - z\partial_r Q^{B(1)} &= G(\theta, r, s, z) Q^{B(0)}, \end{aligned} \quad (10)$$

the solution of which must match the outer solution. The latter varies only weakly on the scale of r and therefore a first order Taylor expansion at the boundary yields the matching condition $Q^B(r, z, s) = Q(\theta, z, s) + kr\partial_y Q(\theta, z, s)$, illustrated in Figure 1B. We note with $Q^{(0)}(\theta, s) = 0$ that the zeroth order $Q^{B(0)}$ vanishes. Inserting (5) into the matching condition, with $-\frac{1}{2}\partial_y Q^{(0)}(\theta, s) = \nu_y^{(0)}(\theta, s) \equiv \nu_y^{(0)}(s)$ the instantaneous flux in the white-noise system, the first order takes the form

$$Q^{B(1)}(r, z, s) = Q_0^{(1)}(\theta, s) + 2\nu_y^{(0)}(s)(z - r). \quad (11)$$

The vanishing zeroth order implies with (10) for the first order $LQ^{B(1)} - z\partial_r Q^{B(1)} = 0$. Appendix B of Kłosek and Hagan [14] states the solution of the latter equation satisfying the half-range boundary condition

$$Q^{B(1)}(r, z, s) = C(s) \left(\frac{\alpha}{2} + z - r + \sum_{n=1}^{\infty} b_n(z) e^{\sqrt{2n}r} \right), \quad (12)$$

with $\alpha = \sqrt{2}|\zeta(\frac{1}{2})|$ given by Riemann's ζ -function and b_n proportional to the n -th Hermite polynomial. We equate (12) to (11) neglecting the exponential term decaying on a small length scale, so that the term proportional to $z - r$ fixes the time dependent function $C(s) = 2\nu_y^{(0)}(s)$ and hence the boundary value $Q_0^{(1)}(\theta, s) = \alpha\nu_y^{(0)}(s)$. This yields the central result of our theory: The effective FPE (8) has the time-dependent boundary condition

$$\tilde{P}(\theta, s) = k\alpha\nu_y^{(0)}(s), \quad (13)$$

reducing the colored-noise problem to the solution of a one-dimensional FPE. The boundary condition can be understood intuitively, as the filtered noise slows down the diffusion at the absorbing boundary with increasing k ; the noise spectrum and the velocity of y are bounded, so in contrast to the white-noise case, there can be a finite density at the boundary. Its magnitude results from a momentary equilibrium of the escape and the flow towards the boundary ($\propto \nu_y^{(0)}$). Considering a shift in the threshold $\tilde{\theta} = \theta + k\frac{\alpha}{2}$, we perform a Taylor expansion of the effective density $\tilde{P}(\tilde{\theta}, s) = \tilde{P}(\theta, s) + k\frac{\alpha}{2}\partial_y\tilde{P}(\theta, s) + O(k^2) = O(k^2)$, where we used (13) and $\partial_y\tilde{P}(\theta, s) = -2\nu_y^{(0)}(s) + O(k)$. In conclusion, to first order in k the dynamic boundary condition (13) can be rewritten as a perfectly absorbing (white-noise) boundary at shifted $\tilde{\theta}$. For the particular problem of the stationary MFPT this was already found by Kłosek and Hagan [14] and Fourcaud and Brunel [16] as a corollary deduced from the steady state density rather than as the result of a generic colored-noise approximation. The recently observed phenomenon of noise-enhanced stability of a meta-stable state exhibits a similar shift of the critical initial position as a function of the color of the noise [20], whereas in some non-linear systems without absorbing boundaries, the color of the noise can effectively be treated as a reduction of the noise intensity [21]. In systems where the dynamic variable is after each escape reset to a value R , an analog calculation [22] yields the additional boundary condition $\tilde{P}(R+, s) - \tilde{P}(R-, s) = k\alpha\nu_y^{(0)}(s)$, which to first order in k is equivalent to a white-noise boundary condition $\tilde{P}(\tilde{R}+, s) - \tilde{P}(\tilde{R}-, s) = O(k^2)$ at shifted reset $\tilde{R} = R + k\frac{\alpha}{2}$.

We now apply the theory to the LIF model exposed to filtered synaptic noise to derive a novel first order correction for the input-output transfer function up to moderate frequencies. This complements the earlier obtained

limits for modulations at high frequencies [15, 16]. While for slow noise, an adiabatic approximation for the transfer function is known [23], for fast noise this is a qualitatively new result, since Fourcaud and Brunel [16] claim that the first order correction to the transfer function vanishes. The corresponding system of coupled differential equations $\tau\dot{V} = -V + I + \mu$ and $\tau_s\dot{I} = -I + \sigma\sqrt{\tau}\xi$ [16] describes the evolution of the membrane potential V and the synaptic current I driven by input with mean μ and variance σ^2 in diffusion approximation. Note that this system can be obtained from (1) by introducing the coordinates $y = \frac{V-\mu}{\sigma}$, $z = \frac{k}{\sigma}I$, and the linear choice $f(y, s) = -y$. Using $x = \sqrt{2}y$ and the marginalized density $\rho(x, s) \equiv \frac{1}{\sqrt{2}}\tilde{P}(x/\sqrt{2}, s)$, we get the reduced effective system (8)

$$\begin{aligned} \partial_s \rho(x, s) &= -\partial_x \Phi(x, s) \equiv \mathcal{L}_0 \rho(x, s) \\ \Phi(x, s) &= -(x + \partial_x) \rho(x, s). \end{aligned} \quad (14)$$

With the function $u(x) = e^{-\frac{1}{2}x^2}$ the right hand side can be transformed to the Hermitian form $\partial_s q(x, s) = -a^\dagger a q(x, s)$, where $q(x, s) = u^{-1}(x)\rho(x, s)$ and we defined the operators $a \equiv \frac{1}{2}x + \partial_x$, $a^\dagger \equiv \frac{1}{2}x - \partial_x$ satisfying $[a, a^\dagger] = 1$ and $a^\dagger a (a^\dagger)^n q_0 = n(a^\dagger)^n q_0$, as in the quantum harmonic oscillator.

We now consider the response properties of the LIF model to a periodic perturbation, i.e. its transfer function. We first simplify the derivation for white noise [24, 25] by exploiting the analogies to the quantum harmonic oscillator introduced above [22] and then study the effective system for colored noise. To linear order a periodic input with $\mu(t) = \mu + \epsilon\mu e^{i\omega t}$ and $\sigma^2(t) = \sigma^2 + H\sigma^2 e^{i\omega t}$ modulates the firing rate $\nu_0(t)/\nu_0 = 1 + n(\omega)e^{i\omega t}$, proportional to the transfer function $n(\omega)$. With a perturbation ansatz for the modulated density $\rho(x, s) = \rho_0(x) + \rho_1(x, s)$ and the separation of the time dependent part, $\rho_1(x) e^{i\omega\tau s}$ follows a second order linear differential equation $i\omega\tau \rho_1 = \mathcal{L}_0 \rho_1 + \mathcal{L}_1 \rho_0$. Here $\mathcal{L}_1 = -G\partial_x + H\partial_x^2$ is the perturbation operator, the first term of which originates from the periodic modulation of the mean input with $G = \sqrt{2}\epsilon\mu/\sigma$, the second from the modulation of the variance. In operator notation the perturbed FPE transforms to $(i\omega\tau + a^\dagger a) q_1 = (G a^\dagger + H (a^\dagger)^2) q_0$ with the particular solution

$$q_p = \frac{G}{1 + i\omega\tau} a^\dagger q_0 + \frac{H}{2 + i\omega\tau} (a^\dagger)^2 q_0,$$

showing that the variation of μ contributes the first excited state, the modulation of σ^2 the second. The homogeneous solution q_h can be expressed as a linear combination of parabolic cylinder functions $U(i\omega\tau - \frac{1}{2}, x)$, $V(i\omega\tau - \frac{1}{2}, x)$ [25, 26]. Finally the boundary conditions on the density and on the flux determine the transfer

function

$$n(\omega) = \frac{G}{1 + i\omega\tau} \frac{\Phi'_\omega|_{x_\theta}^{x_R}}{\Phi_\omega|_{x_\theta}^{x_R}} + \frac{H}{2 + i\omega\tau} \frac{\Phi''_\omega|_{x_\theta}^{x_R}}{\Phi_\omega|_{x_\theta}^{x_R}}, \quad (15)$$

where $x_{\{R,\theta\}} = \sqrt{2} \frac{\{R,\theta\} - \mu}{\sigma}$ and we introduced $\Phi_\omega(x) = u^{-1}(x) U(i\omega\tau - \frac{1}{2}, x)$ as well as $\Phi'_\omega = \partial_x \Phi_\omega$ to obtain the known result [15, 24, 25].

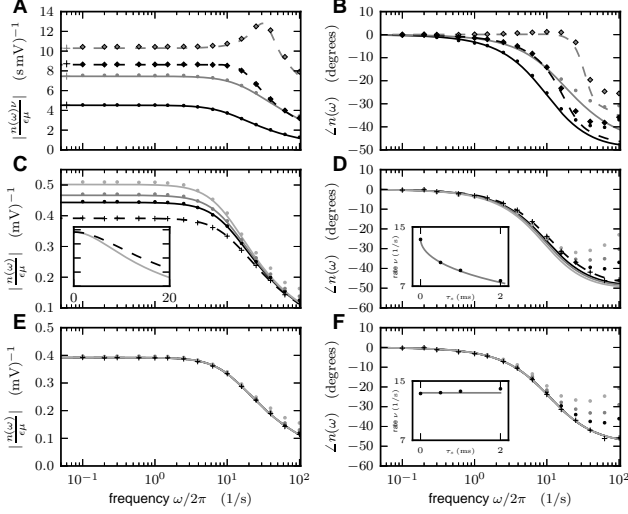


Figure 2. Dependence of transfer function of LIF model on synaptic filtering. Absolute value (left column) and phase (right column) of the transfer function for $\theta = 20$ mV, $V_r = 15$ mV, $\tau_m = 20$ ms. Upper row (A,B): $\tau_s = 0.5$ ms, $\sigma = 4$ mV (solid), $\sigma = 1.5$ mV (dashed), firing rate $\nu = 10$ Hz (black) and $\nu = 30$ Hz (gray). Analytical prediction \tilde{n} (solid curves), direct simulations (dots, diamonds), and zero frequency limit $\frac{d\nu}{d\mu}$ (crosses). Middle row (C,D): $\sigma = 4$ mV, white noise (dashed), colored noise $\tau_s \in [0.5, 1, 2]$ ms (from black to gray) and $\tau_s = 2$ ms normalized to zero frequency limit of white noise (gray, inset). Lower row (E,F): same as (C,D) but threshold and reset shifted $\{\theta, R\} \rightarrow \{\theta, R\} - \sqrt{\tau_s/\tau} \frac{\alpha}{2}$ to maintain constant firing rate.

With the general theory developed above we directly obtain an approximation for the colored-noise transfer function n_{cn} , replacing $x_{\{R,\theta\}} \rightarrow x_{\{\tilde{R},\tilde{\theta}\}}$ in the white-noise solution (15), denoted by \tilde{n} . Note that we here only consider a modulation of the mean μ , which dominates the response properties. Treating a modulation of the variance σ^2 is difficult within our approach since there is no corresponding choice of f in (1). A Taylor expansion of the resulting function around the original boundaries $x_{\{R,\theta\}}$ reveals the first order correction in k

$$n_{cn}(\omega) = n(\omega)|_{H=0} + \sqrt{\frac{\tau_s}{\tau}} \frac{\alpha}{\sqrt{2}} \frac{G}{1 + i\omega\tau} \left(\frac{\Phi''_\omega|_{x_\theta}^{x_R}}{\Phi_\omega|_{x_\theta}^{x_R}} - \left(\frac{\Phi'_\omega|_{x_\theta}^{x_R}}{\Phi_\omega|_{x_\theta}^{x_R}} \right)^2 \right), \quad (16)$$

valid for arbitrary noise intensity σ entering the expression via the boundaries $x_{\{R,\theta\}}$. The first correction term is similar to the H -term in (15); colored noise has a similar effect on the transfer function as a modulation of the variance [25] in the white-noise case. For infinite frequencies this similarity was already found: modulation of the variance leads to finite transmission at infinite frequencies in the white-noise system [25]. The same is true for modulation of the mean in the presence of filtered noise [15]. However, for infinite frequencies our analytical expression behaves differently. The two correction terms in the second line of (16) cancel each other, since $\Phi''_\omega \rightarrow (i\omega\tau)^2 \Phi_\omega$ and $\Phi'_\omega \rightarrow (i\omega\tau)^2 \Phi_\omega^2$. Thus the transfer function decays to zero as in the white-noise case. These deviations originate from neglecting the time derivative on the left hand side of (9) that is of order k^2 only up to moderate frequencies $\omega\tau k \ll 1$. The high frequency limit $\omega\tau k \gg 1$ is known explicitly [15], but it was shown that the finite high-frequency transmission is due to the artificial hard threshold in the LIF model [27, 28]. The upper panels in Figure 2 show a comparison of the analytical prediction (16) to direct simulations for different noise levels σ and firing rates controlled by mean μ . The analytical absolute value is in agreement with the simulations for the displayed range of frequencies. Above 100 Hz deviations occur as expected. However, these are less important, since our theory predicts the response properties well in the frequency range where transmission is high. The deviations are more pronounced and already observed at lower frequencies in the phase shift. At high firing rate and low noise, the neuron is mean driven and exhibits a resonance at its firing frequency, again well predicted by the analytical result. The middle and the lower row show a comparison to the white-noise case. A qualitative change can be observed: synaptic filtering on the one hand increases the dc-susceptibility counter to the behavior of the decreasing firing rate (inset in panel D). On the other hand the cutoff frequency (inset in panel C) is reduced. Our theory fully explains these qualitative changes by a shift in the reset and the threshold as shown explicitly in panel E: for different synaptic time constants the response in the low frequency regime is not altered in comparison to the white-noise case if reset and threshold are adapted to compensate for the effect of colored noise.

The analytical expression (16) has immediate applications: The transmission of correlated activity by pairs of neurons exposed to common input [29] can now be studied in a time-resolved manner. On the network level, the theory of correlated activity (reviewed in [30]) relies on the transfer function and also the stability of networks and emerging oscillations [24] become analytically tractable for the case of realistic synaptic filtering. For these experimentally observable phenomena the transmission of frequencies up to $\simeq 100$ Hz is most relevant and an analytical prediction has not been available prior to the present work.

This work was partially supported by HGF young investigator's group VH-NG-1028, Helmholtz portfolio theme SMHB, Juelich Aachen Research Alliance (JARA), EU Grant 269921 (BrainScaleS), and EU Grant 604102 (Human Brain Project, HBP). All simulations were carried out with NEST (<http://www.nest-initiative.org>). We thank two anonymous referees for their constructive comments which helped us to substantially improve the manuscript.

-
- [1] H. Kramers, *Physica* **7**, 284 (1940).
 - [2] F. Moss and P. V. E. McClintock, eds., *Noise in Non-linear Dynamical Systems*, vol. 1 (Cambridge University Press, 1989).
 - [3] C. W. Gardiner, *Handbook of Stochastic Methods for Physics, Chemistry and the Natural Sciences* (Springer-Verlag, Berlin, 1983).
 - [4] J. B. Johnson, *Phys. Rev.* **32**, 97 (1928).
 - [5] H. Nyquist, *Phys. Rev.* **32**, 110 (1928).
 - [6] F. Moss and P. V. E. McClintock, eds., *Noise in Non-linear Dynamical Systems*, vol. 2 (Cambridge University Press, 1989).
 - [7] F. Moss and P. V. E. McClintock, eds., *Noise in Non-linear Dynamical Systems*, vol. 3 (Cambridge University Press, 1989).
 - [8] J. M. Sancho, M. S. Miguel, S. L. Katz, and J. D. Gunton, *Phys. Rev. A* **26**, 1589 (1982).
 - [9] K. Lindenberg and B. J. West, *Physica A* **119**, 485 (1983).
 - [10] P. Hanggi, T. J. Mroczkowski, F. Moss, and P. V. E. McClintock, *Phys. Rev. A* **32**, 695 (1985).
 - [11] R. F. Fox, *Phys. Rev. A* **33**, 467 (1986).
 - [12] P. Grigolini, *Phys. Lett.* **119**, 157 (1986).
 - [13] C. R. Doering, P. S. Hagan, and C. D. Levermore, *Phys. Rev. Lett.* **59**, 2129 (1987).
 - [14] M. M. Klosek and P. S. Hagan, *J. Math. Phys.* **39**, 931 (1998).
 - [15] N. Brunel, F. S. Chance, N. Fourcaud, and L. F. Abbott, *Phys. Rev. Lett.* **86**, 2186 (2001).
 - [16] N. Fourcaud and N. Brunel, *Neural Comput.* **14**, 2057 (2002).
 - [17] H. Risken, *The Fokker-Planck Equation* (Springer Verlag Berlin Heidelberg, 1996).
 - [18] P. Hänggi, P. Jung, and P. Talkner, *Phys. Rev. Lett.* **60**, 2804 (1988).
 - [19] C. R. Doering, R. J. Bagley, P. S. Hagan, and C. D. Levermore, *Phys. Rev. Lett.* **60**, 2805 (1988).
 - [20] A. Fiasconaro and B. Spagnolo, *Phys. Rev. E* **80**, 041110 (2009).
 - [21] D. Valenti, G. Augello, and B. Spagnolo, *The European Physical Journal B* **65**, 443 (2008), ISSN 1434-6028.
 - [22] J. Schuecker, M. Diesmann, and M. Helias, arXiv pp. 1410.8799v1 [q-bio.NC] (2014).
 - [23] R. Moreno-Bote and N. Parga, *Phys. Rev. Lett.* **96**, 028101 (2006).
 - [24] N. Brunel and V. Hakim, *Neural Comput.* **11**, 1621 (1999).
 - [25] B. Lindner and L. Schimansky-Geier, *Phys. Rev. Lett.* **86**, 2934 (2001).
 - [26] M. Abramowitz and I. A. Stegun, *Handbook of Mathematical Functions: with Formulas, Graphs, and Mathematical Tables* (Dover Publications, New York, 1974).
 - [27] B. Naundorf, T. Geisel, and F. Wolf, arXiv pp. arXiv:physics/0307135 [physics.bio-ph] (2003).
 - [28] N. Fourcaud-Trocme, D. Hansel, C. van Vreeswijk, and N. Brunel, *J. Neurosci.* **23**, 11628 (2003).
 - [29] E. Shea-Brown, K. Josic, J. de la Rocha, and B. Doiron, *Phys. Rev. Lett.* **100**, 108102 (2008).
 - [30] D. Grytskyy, T. Tetzlaff, M. Diesmann, and M. Helias, *Front. Comput. Neurosci.* **7**, 131 (2013).